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Structure of northern spotted owl nest stands and their historical conditions on the eastern slope of the Pacific Northwest Cascades, USA

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Abstract

The northern spotted (*Strix occidentalis caurina*) uses a wide array of nesting habitat throughout its current range and successfully reproduces in a variety of stand types on the eastern slope of the Pacific Northwest Cascades. The species has the ability to utilize dynamic forest stands that continue to undergo significant changes in tree density, proportion of tree size classes, and tree species composition. Current stand structure and composition reflect the results of timber harvest, reduced fire effects and ongoing successional and stand development processes. In nest stands, multi-layered canopy was more strongly expressed in numbers of both small (< 13 cm DBH) and large (> 41 cm DBH) trees than in unoccupied stands of the same type within the owl neighborhoods. Tree density and the proportion of shade-tolerant tree species have increased significantly in spotted owl nest sites in both dry and wet forests since Eurosettlement. Barring disturbance, further increases in the dominance of shade-tolerant species should occur over time with continual change in nest stand structure and composition. The development of dense forest stands and 'old-forest structural attributes' as a result of reduced fire effects could be potential mitigating factors to the loss of old-forest habitat from harvest and should be considered in determining the available owl habitat in the eastern Cascades. However, old-forest structural attributes in dense, overstocked stands are at high fire hazard and should be viewed as transitional until old-forest habitat with improved sustainability becomes available. © 1997 Elsevier Science B.V.

Keywords: Forest disturbance; Habitat; Nest sites; Owl neighborhoods

1. Introduction

Conservation of northern spotted owl (*Strix occidentalis caurina*) habitat depends on knowledge of habitat characteristics, field identification, and appropriate management. The Interagency Scientific Committee for the Conservation of the Northern Spotted Owl identified the lack of and the specific need for detailed information on stand structure of nesting, roosting, and foraging habitat (Thomas et al., 1990).

Nest stand habitat conservation is of particular importance due to extensive owl use during the breeding season. Previous descriptions of northern spotted owl nest stands in forests west of the Cascades have characterized forest structure as mature to old-growth forests (Forsman et al., 1984; LaHaye, 1988). In western Oregon, 95% of 123 paired owls were found in undisturbed old-growth forests (Forsman, 1976). East of the Cascades, however, only 27% of owl nest stands were found in old growth with the remainder

in various stages of stand development (Buchanan et al., 1995).

Insect, disease, and fire disturbance effects limited the proportion of old forests east of the Cascade Crest prior to Eurosettlement (Camp, 1995). Previous fire history analysis of six spotted owl nest stands indicated a fire frequency of approximately 13 years prior to 1900, and fire absence from 1900 to 1990 (Everett et al., 1992). The reduction in fire effects and livestock grazing caused significant increases in tree density and subsequent stand development created multiple canopy-layered forests in dry pine/Douglas-fir forests of the inland west (Covington et al., 1994). Altered disturbance regimes in spotted owl habitat in the eastern Cascades was described in general terms by Agee and Edmonds (1992). However, no description of structural or compositional changes in spotted owl nest stands from pre-Eurosettlement to current conditions was found in the literature.

Heterogeneous topographic, edaphic, and climatic conditions east of the Cascade Crest provide a diverse mixture of tree series and plant associations in an array of successional and developmental stages (Franklin and Dyrness, 1973). Close to the crest, where precipitation can exceed 229 cm (90 in) per year, wet forest series include western hemlock (*Tsuga heterophylla*-TSHE); mountain hemlock (*T. mertensiana*-TSME), red cedar (*Thuja placata*-THPL), noble fir (*Abies procera*-ABPR), and Pacific silver fir (*A. amabilis*-ABAM). Eastward, in the rain shadow of the Cascades, the wetter site plant associations of the grand fir (*A. grandis*) series (grand fir/vine maple (*Acer circinatum*-ABGR/ACCI) and grand fir/vanilla leaf (*Achylys triphylla*-ABGR/ACTR) give way to drier grand fir plant associations and finally Douglas-fir (*Pseudotsuga menziesii*-PSME) and ponderosa pine (*Pinus ponderosa*-PIPO) series in a 50 to 76 cm (20 to 30 in) precipitation zone (Franklin and Dyrness, 1973; Lillybridge et al., 1995).

Northern spotted owls are found in a variety of forest zones in Washington, Oregon, and Northern California (Thomas et al., 1990; Gutierrez, 1992). In eastern Washington, northern spotted owls occur from the wet fir-hemlock forests along the Cascade Crest to the dry ponderosa pine/Douglas-fir forests on the east slope foothills (Hanson et al., 1993). To

manage owl habitat throughout the existing range, as required by the Endangered Species Act of 1973, the structural and compositional characteristics of nest stands in this broad array of tree series needs to be defined. Sufficient numbers of studies have been done to identify common attributes associated with spotted owl nesting habitat such as multi-layered and multi-species canopy, canopy closure, mistletoe infestation (interior Northwest) and the presence of remnant large trees, snags and logs, but specific characteristics of each attribute vary across the owl's range (Thomas et al., 1990; Lujan et al., 1992).

Buchanan et al. (1993) conducted a detailed analysis of 85 of 102 known nest sites on the eastern slope of the Washington Cascades. Using a nest tree or random tree-centered sampling plot, they found nest tree sites had a greater number of larger diameter trees, greater basal area of live trees, and greater number of Class IV snags (broken tops, with minimal branches and bark) than random tree sites in the same stand. They classified nest stands into the Oliver (1981) general stand development phases, but the description remains somewhat ambiguous because stand structure and composition can vary significantly within phase types. Also, the tree-centered sampling scheme that was required for nest site characterization could introduce a crown cover bias in the characterization of nest stands that had less than 100% crown closure.

We sampled a subset of these nest stands that had successfully-reproducing owl pairs to develop a more detailed classification of nest stand types, and to compare nest stand structure with the same but unoccupied stand type within an owl neighborhood. The owl neighborhood was defined as stands within a 900 m (2900 ft) radius of the nest tree. Also, we described and compared current and estimated historical nest site conditions. Our null hypotheses for this study were: (1) stand structure does not vary significantly among current spotted owl nest stands in the eastern Cascades; (2) that structure and composition of current nest sites are not significantly different from their pre-Eurosettlement conditions; and (3) that reproductively-successful owl nest stands do not have, singly or in combination, greater tree densities, basal area, mistletoe infestation, or snag and log loadings than the same but unoccupied stand type within the owl neighborhood.

2. Methods

2.1. Field plots

A total of 48 nest stands on the eastern slope of the Cascades, with identified nest trees and successfully-reproducing spotted owls pairs, were sampled from 1990 to 1992. Twenty-four of these nest stands were randomly selected for study on the Wenatchee and Okanogan National Forests. These sites were supplemented by a total population sample of 11 nest stands in the Swauk Drainage, Wenatchee NF (previous owl telemetry research area), a total population sample of seven nest stands on private property (Boise Cascade lands), and a total population sample of six nest stands (those with identified nest sites) on the Deschutes National Forest in eastern Oregon.

Nest tree locations were plotted on 1:12 000 color aerial photos and a scanning stereoscope used to identify nest stand boundaries. Stands were sampled at a rate of one plot per every 1.2 ha (3 acres) with a minimum of four and a maximum of 12 plots distributed randomly (azimuth and distance) along transects that covered the extent of the stand. Each plot was characterized by slope, aspect, elevation, topographic position, degree of infestation by mistletoe, presence of fire scars, and cut stumps from historical logging. Fixed [0.02 ha (0.05 acre)] plots were used to sample densities of trees, snags and logs, and variable radius (20 BAF) plots used to estimate basal area. Forest structure variables recorded at each plot included: basal area, crown density, species, diameter at breast height (DBH), and height for all trees and snags. Tree species and diameter of cut stumps were recorded as well as decay class for logs [> 15 cm (6 in) dia.] (Sollins, 1982) and snags [> 25 cm (10 in) diam.] (Cline et al., 1986). Each nest stand was searched for fire scars and up to eight scars were sectioned for analysis of fire-return interval. Fire scars were dated to define the fire-free interval and the date of the last fire-free interval prior to reduced fire effects (Arno and Sneek, 1977). The sampling procedure was applied uniformly in all nest stands and similar unoccupied stands in the neighborhood surrounding the nest tree.

At the nest tree a 0.02 ha fixed plot was established and all trees, snags, and logs within the plot were described by species, DBH, height, and age.

This plot was expanded to 0.1 ha (0.25 acre) to sample trees, snags, and logs > 23 cm (9 in) diam. Age of each tree > 5 cm DBH was determined from two perpendicular increment cores at breast height. An increment core was taken at ground level for each size class to estimate years required for trees to grow to breast height. Ages of stems < 5 cm DBH were estimated from cross sections taken from 10% of the trees in this size class. Coarse woody debris decay rates reported for the eastern slope of the Cascades are sufficiently slow (Maser et al., 1979; Erickson et al., 1985) such that decay class IV or V snags and logs > 15 cm (6 in) would be considered part of the historical stand because the decay period equaled or exceeded the time from the last major fire event. To determine if hard (decay Class II or III) standing snags were living components of the historical forest [100 years before the present (BP)], the snag age at mortality was added to one half the estimated snag retention period and the sum checked against the time period since the date of the last fire. Snag retention periods were estimated for each species and size class from a snag retention model based on 22 eastern Washington Cascades burn sites ranging from 2 to 80 years (Leuschen, 1996). Ages of decay Class II and III logs were determined or estimated from DBH and the age at mortality was added to the total estimated snag retention period to determine their presence or absence and size in the historical stand. The integration of these data provided a valid basis for estimating historical stand structure prior to Eurosettlement, but we recognize future revisions are probable as more detailed decay rate information is developed.

2.2. Data analysis

Data analysis included: (1) classification and analysis of nest stand types; (2) comparison of historical and current nest site conditions; and (3) a comparison of nest stand characteristics with similar unoccupied stands in the same owl neighborhood. Stand data minus nest tree plots was run in cluster analysis (BMDP, 1992) to group similar stand types by tree size-class density. To increase our confidence in cluster results, multiple clustering algorithms [single linkage, centroid linkage (BMDP, 1992)] and resemblance matrix indices [Euclidean distance, Bray and Curtis, and Correlation (BMDP, 1992)] were evalu-

ated for consistency. Standardized data sets [Z score = observed/maximum observed (Romesburg, 1984)] were used to reduce variability among stands. Discriminate analysis was used to evaluate the number of stands correctly classified into groups and to define the major discriminate variables among stand types. Derived nest stand groups were compared for differences in tree density by six size classes: seedlings, up to 3 cm (1 in) diam.; saplings, 3 to 13 cm (1 to 5 in) DBH; poles, 13 to 23 cm (5 to 9 in); small trees, 23 to 41 cm (9 to 16 in); medium trees, 41 to 64 cm (16 to 25 in); and large trees, greater than 64 cm (25 in), and differences in snags > 23 cm (9 in) and logs > 23 cm (9 in) using multivariate analysis of variance (MANOVA), and analysis of variance (ANOVA) procedures (BMDP, 1992). Brown-Forsythe and Welch statistics that are robust to inequality of variances were used in lieu of the analysis of variance *F* test if variances were not homogeneous (Leven's test statistic) (BMDP, 1992). A square root or arc sine transformation of the data was used to reduce skewness and kurtosis when present (Little and Hills, 1978). Student-Newman-Keuls multiple comparison was used for selected mean comparisons as opposed to Bonferroni *P* values based on all possible mean comparisons (BMDP, 1992). These statistical procedures were also used in comparing nest stands to similar unoccupied stands in the same owl neighborhood.

Nest sites were grouped according to the nest stand types in which they occurred and clustered using small, medium and large tree densities as variables. Through reiterative discriminate analysis classifications, nest site groups were derived with > 80% structural similarity within groups. Paired data sets of historical (pre-Eurosettlement) and current forest structure for the same nest stand were standardized and compared in *t*-tests. Differences in tree density between current and historical stands in wet and dry forests settings were similarly evaluated.

3. Results and discussion

3.1. Current nest stand characteristics

Cluster analysis using density of small (seedlings and saplings), medium (poles and small trees) and

large (medium and large trees) diameter trees as cluster variables and an 80% within-cluster similarity cut point provided 11 initial spotted owl nest stand types. Discriminate analysis of these groupings reduced the number of stand types to nine with a successful overall classification rate of 98% and with no group having less than 92% correct stand classification (Fig. 1). Density of small trees was the dominant discriminating factor among clusters followed by medium- and then large-sized trees. Approximately 70% of the stands sampled were Stand Types 3 (18.8%), 5 (14.6%), 6 (14.6%) and 8 (25%). Approximately 18.6% of the sampled stands were Stand Types 2, 4, 7, and 9 (6.2% each); and Stand Type 1 occurred the least often (2.2%).

Stand types in Fig. 1 are arrayed according to increased stand development from immediately following stand-replacement disturbance to old-forest structure. Using the stand development classification by Oliver (1981), stands were classified as stand initiation (tree establishment following stand-replacement disturbance), stem exclusion (competition-induced tree mortality), understory reinitiation (establishment of understory tree species), and old-forest (ongoing process of understory reinitiation and stem exclusion of the most shade-tolerant dominant species). A majority of stands were in stem exclusion (46%) and understory reinitiation (40%) phases with old-forest (12%) and stand initiation (2%) phases occurring less often. The single stand represented in Stand Type 1 is in the stand initiation phase following recent harvest disturbance. Stands in Types 2 and 7 are in the stem exclusion phase and Stand Type 6 is comprised mostly (86%) of stands in this phase. Stand Type 4 has a majority of stands in the understory reinitiation phase (66%). Stand Types 3, 5, and 8 have a combination of stand types in stem exclusion (14 to 56%), understory reinitiation (33 to 67%), and old-forest (8 to 29%) phases. Stand Type 9 is comprised of old-forest (66%) and understory reinitiation (33%) phases.

Differences between these results and those of Buchanan et al. (1995) who reported 17% of nest stands in the stem exclusion phase, can be ascribed to our broader criteria that stem exclusion is in process if the time interval since the last seedling recruitment exceeds the range in seedling ages. Conversely, our smaller proportion of old-forest stands

(12 vs. 27%) can be ascribed to Buchanan et al.'s (1995) use of a broader definition of old-forest. Our old-forest definition had the additional caveat that seedling reinitiation of the most shade-tolerant tree species of the plant association should have been reached in stand development. Both our results and those of Buchanan et al. (1995) suggest that eastern Cascade spotted owl nest stands are highly variable in stand development stage and that a preponderance of nest stands are not characterized by old-forest structure. These results are in sharp contrast to nesting sites in western Oregon and the Olympic Peninsula in Washington where only 4% of 130 nest sites occurred in mature or younger stands (Thomas et al., 1990)

Sampled nest stands occurred predominantly

(92%) in grand fir (ABGR) or Douglas-fir (PSME) forest series. Approximately 79% of all sampled nest stands were in ABGR series, with 50% of nest stands in dry ABGR and 29% in wet ABGR plant associations. Only three nest stands occurred in western hemlock (TSHE), red cedar (THPL), and Pacific silver fir (ABAM) series. As expected, the structure of a given stand type occurred in more than one tree series. Stand Types 1, 3, and 4 occurred in the ABGR series (dry plant associations), and Stand Types 2 and 7 were represented in both PSME and ABGR series. Stand Type 6 was represented in the ABGR (both wet and dry plant associations), PSME, and TSHE series. Stands in Stand Types 5, 8 and 9 were mostly in wet ABGR, TSHE, or ABAM series.

Multiple species canopy existed in all nest stand

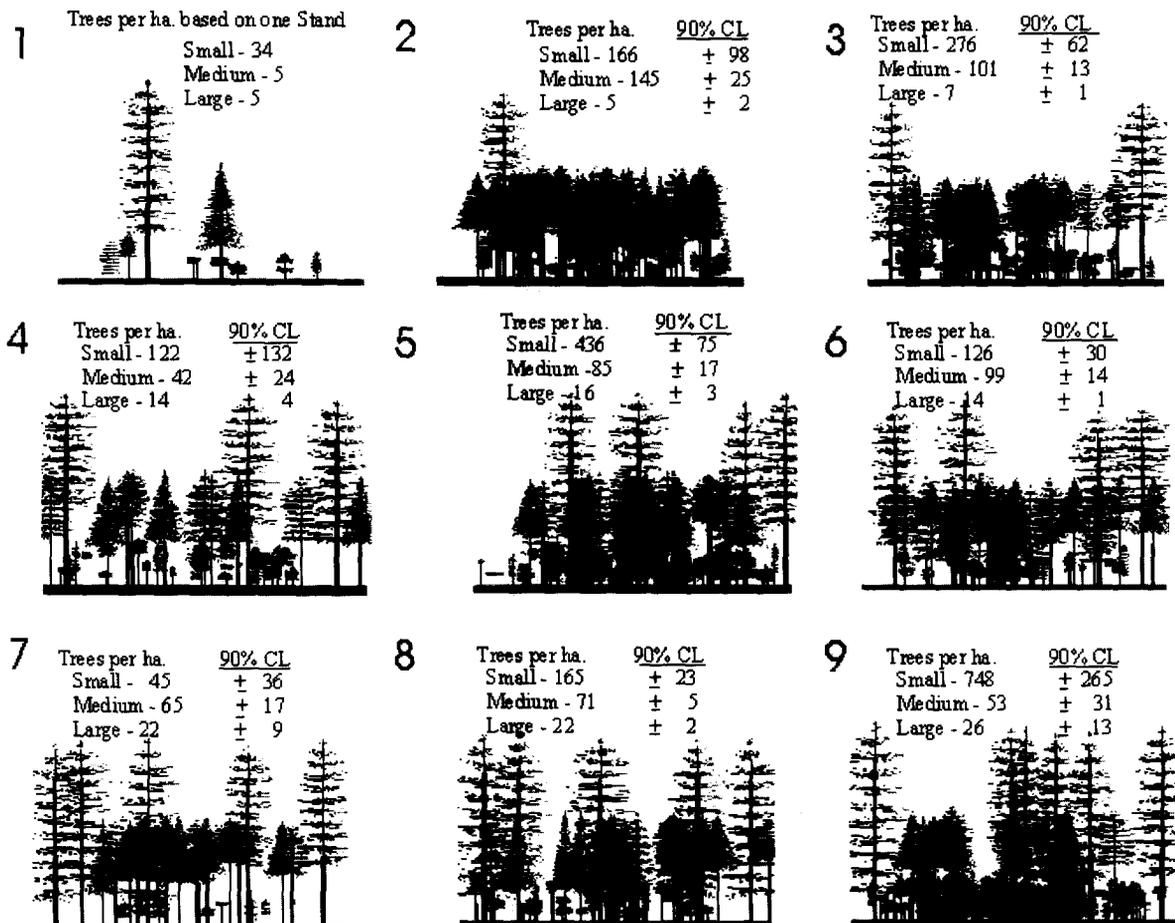


Fig. 1. Nine structural spotted owl nest stand types defined by cluster and discriminate analysis procedures. Small class includes seedlings and saplings; medium class includes poles and small trees; large includes medium and large trees.

types, with stand type 1 having the least species diversity (Fig. 2). Early seral species PIPO and PSME predominated in the large tree size class of all stand types except 5 and 9 where shade-tolerant species ABAM, ABGR, ABPR, or TSME made up a significant portion of the overstory. The maximum

PSME density was 20 trees per ha (50 trees per acre) in Stand Type 7 and this was significantly ($P = 0.1$ to 0.01) greater than the 4 to 11 trees per ha (10 to 28 trees per acre) in other stand types. Maximum large PIPO density of five trees per ha (12 trees per acre) occurred in Stand Type 1 with no large PIPO

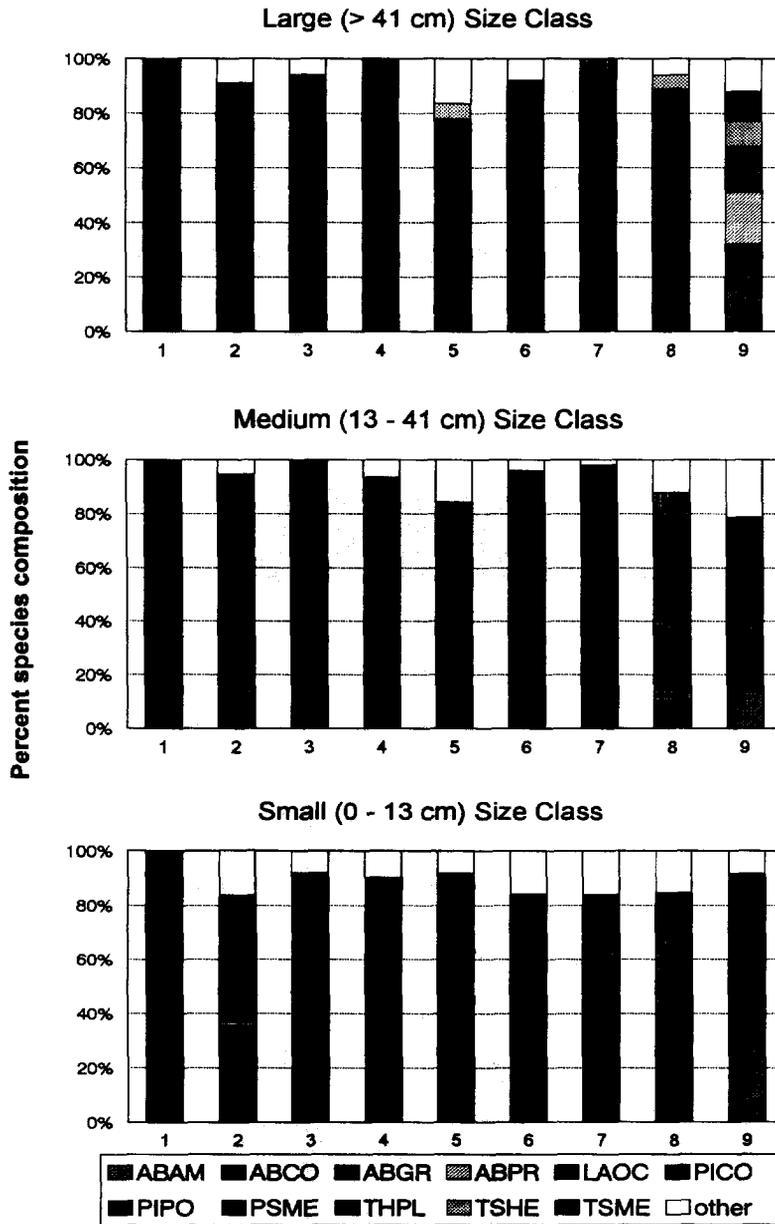


Fig. 2. Species composition of small (seedlings and saplings), medium (poles and small trees), and large (medium and large trees) trees by stand type.

in the old-forest Stand Type 9. More shade-tolerant ABGR had maximum density in Stand Type 9, six trees per ha (16 trees per acre), and this was significantly greater ($P = 0.5$) than other stand types except Stand Types 5 and 8.

In the medium tree size class, the proportion (albeit not the number) of PIPO and PSME declined and the representation of shade-tolerant ABGR and ABCO increased. PIPO had a maximum of seven trees per ha (18 trees per acre) in Stand Type 7 and again no representation in old-forest Stand Type 9. The PSME series had a maximum tree density in Stand Type 2, 66 trees per ha (164 trees per acre), which was significantly greater than in Stands 5, 8, and 9, nine to 18 trees per ha (23 to 46 trees per acre). A maximum of 51 trees per ha (125 trees per acre) of ABGR occurred in Stand Type 5 and densities fell significantly ($P = 0.05$, > 1 tree per ha) in Stand Type 7.

In the small tree category, ABGR density reached 392 trees per ha (968 trees per acre) in the old-forest Stand Type 9 and this was significantly ($P = 0.05$) greater than in the other stand types, 0 to 104 trees per ha (0 to 257 trees per acre) except Stand Types 3 and 5, 177 to 334 trees per ha (436 to 824 trees per acre). Fewer small trees of PSME were present; a maximum of 70 trees per ha (174 trees per acre) occurred in Stand Type 3. There were 0 to 48 trees per ha (0 to 118 trees per acre) in the other stand types. The maximum number of small PIPO trees was less than PSME or ABGR, 30 trees per ha (74 trees per acre) and occurred in Stand Type 1. Small tree PIPO densities were two to seven trees per ha (four to 17 trees per acre) in the other stand types. More shade-tolerant species THPL and ABCO were never the major species in the small size class, but were present in four stand types.

The dominant large tree species and the most shade-tolerant understory species were the same in only six of 48 nest stands. Unless nest stands are disturbed, future species composition of nest stands will differ from current conditions and eventually become dominated by the shade-tolerant understory species (79% of stands were in the ABGR series as discussed above). Given that the majority of spotted owl nest trees in eastern Washington, Oregon and northeastern California occur in PSME (Forsman et al., 1984; LaHaye, 1988; Buchanan et al., 1993), and

without disturbance PSME would be replaced by more shade-tolerant species, we may need to be concerned about the future abundance of nest trees.

Current nest stand structure reflects reduced fire effects, the stand development process, and the occurrence of timber harvest. Fire scars were found in all stand types and in 33 to 100% of the stands within each type. The last burn event occurred between 1838 and 1935 in all stand types except those comprising Stand Type 9 (1590 to 1890). The fire-free interval prior to European settlement was 14.3 to 19.6 years among all stands except Stand Type 9 (400+ years). Using a conservative 20-year fire-free interval, a majority of the stands are three to eight fire-free intervals divergent from pre-European conditions.

Tree harvest occurred in all stand types with the exception of Stand Type 7. Northern spotted owl use of partially harvested forest lands has been previously described (Gutierrez, 1992) and specifically for forests of the eastern Washington Cascades (King, 1993; Buchanan et al., 1995). Our estimates of timber harvest activity for sampled stand types (60%) was greater than the 46% reported by Buchanan et al. (1995) and may reflect different sampled sites or sampling schemes. The opposing processes of increased tree density from reduced fire effects and decreased tree density of larger tree sizes and specific species from selective harvesting have caused structural alterations in nest stands from those that would be expected in pre-Eurosettlement conditions. Because of the more ubiquitous alteration of fire effects across the landscape and the lack of harvesting smaller diameter trees, the net effect has been an increase in tree density from historical conditions.

Stand types varied significantly in numbers of trees per ha from a low of 43 (106 per acre) following tree harvest (Type 1) to 826 (2040 per acre) in old-forest (Type 9) (Table 1). Tree numbers were 1.5 to 10 times greater than those reported for mostly old-forest stands intensively used by northern spotted owls in the Gifford-Pinhot, Mt. Baker-Snoqualmie, and Olympic National Forests in western Washington (Allen et al., 1989; in Thomas et al., 1990). Comparisons between our tree density values and those of Buchanan et al. (1995) are made difficult because we used different size classes. However, our tree density values are much greater than the 69

Table 1
Differences in tree densities (trees ha⁻¹) by size class among stand types

Stand type	1 ^a	2	3	4	5	6	7	8	9
<i>Size class</i>									
Seedlings	7	30	91	34	203	34	11	58	521
Saplings	27	136	185	88	233	91	33	107	227
Poles	4	93	66	24	58	57	28	41	31
Small tree	1	53	35	18	28	42	36	30	21
Medium tree	4	4	6	11	12	12	19	15	15
Large tree	1	<1	<1	4	5	2	4	7	11
Total trees	43	316	384	178	537	238	131	258	826

^a Single stand representation prevented Stand Type 1 inclusion in statistical analysis. Note: mean values in italics are significantly different from the row maximum ($P < 0.05$).

stems per ha (170 stems per acre) reported by Bart and Earnst (1992, from Buchanan (1991)) for ≥ 2 cm (4 inch) DBH stems in nest stands in the eastern Washington Cascades. We believe the difference is a result of variations in sampling design and sites sampled.

Seedlings, saplings, poles, small, medium and large tree densities were significantly ($P < 0.01$) different among nest stand types. Multiple mean comparisons indicate Stand Type 9 had significantly greater seedlings than other stand types; sapling density was greatest in Stand Types 3, 5 and 9; pole density was greatest in Stand Types 2, 3, 5, and 6; small tree density was greatest in Stand Types 2, 3, 6, and 7; medium tree density was greatest in Stands 5, 6, 7, 8, and 9; and large tree density was greatest in Stands 5, 8, and 9 (Table 1). The large number of seedlings and saplings reported for old-forest is in agreement with previous work by Spies and Franklin (1988) who noted the transitory abundance of small understory trees in old-forest stands.

We were unable to show a significant differences ($P = 0.05$) in basal area, 17.5 to 24.2 m² ha⁻¹ (188

to 260 sq ft per acre) or crown cover (83 to 94%) among nest stand types; the low number of replicates of some stand types resulted in a low power of test (probability of recognizing significant difference when present, Neter et al., 1990). Stand Type 1 had lower basal area, 13.8 m² ha⁻¹ (149 sq ft per acre), and lower canopy cover, 55%, than other stand types, but was represented by a single stand and could not be statistically evaluated. Mistletoe occurred on 31% of Douglas-fir trees in sampled nest stands, and there was no significant difference in mistletoe infestation among stand types.

3.2. Nest stands and unoccupied stands

Vertical height diversity has been shown to be associated with spotted owl use (Solis and Gutierrez, 1990). Nest stands had significantly greater numbers of saplings, poles and large trees than unoccupied stands of the same type within the same neighborhood (Table 2). The greater representation of both lower and upper canopy layers may enhance the multi-layer canopy attribute in nest stands. Unoccupied stands with greater numbers of median size trees and fewer large and small trees would tend toward a single-layered canopy with diffuse lower and upper boundaries.

We did not find significant differences in numbers of seedlings, small trees, snags, and logs between similar occupied and unoccupied stands. There was no significant difference in mistletoe infestation between nest stands (31%) and unoccupied stands (42%). The absence of differences in some attributes between nest and unoccupied stands in the same neighborhood may indicate that the sampled stand variables were pervasive throughout the owl neighborhood (Pidgeon, 1995) and that the defining attributes for unoccupied stands were not measured within or external to the stand. Also, nest stands and

Table 2
Stand structural characteristics of nest stands and unoccupied stands of the same type

	Number ha ⁻¹							
	Seedlings	Saplings	Poles	Small	Medium	Large	Snags	Logs
Nest stand	83	156 *	57 *	33	10	3.4 **	10	13
Unoccupied stand	90	143	54	37	11 *	2.2	9	16

*, ** significance at $P = 0.1, 0.05$.

unoccupied stands of the same type in a given neighborhood may represent multiple nest stand opportunities that can not be utilized simultaneously.

We could not demonstrate significant differences in representation of the more prominent tree species ponderosa pine, Douglas-fir, or grand fir between the nest stand and unoccupied stands of the same type within the neighborhood. However, western white pine (*Pinus monticola*) had significantly more seedlings, 3.4 vs. 1 per ha (8.4 vs. 2.0 per acre), $P = 0.1$ and western larch (*Larix occidentalis*) had five times the number of saplings, 1 vs. 0.2 (2.1 vs. 0.6), $P = 0.1$, twice the number of small, 3 vs. 1.5 (7.5 vs. 3.8), $P = 0.05$, and four times the number of medium size trees, 2 vs. 0.5 per ha (4.8 vs. 1.1 per acre) $P = 0.01$, in unoccupied stands than nest stands ($n = 5$ and 11, respectively). These tree species are of low to moderate shade tolerance and their greater representation in unoccupied stands may indicate a previous loss in overstory trees in excess of that in nest stands in the same owl neighborhood.

3.3. Current and historical nest sites

Cluster and discriminate analyses of current nest sites using the nest stand grouping were successful in

less than 45% of the cases and provided an excessive number of groups with single stand representation. Reiterative discriminate analysis procedures provided nine spotted owl nest site groupings (A through I) with > 80% within group similarity. Differences in structure between nest stands and nest sites can not be statistically evaluated because the differences in sampling methods confound comparisons; however, cluster and discriminate analysis results suggest that nest site characteristics are not representative of the stands in which they occur. This speculation is supported by Buchanan et al. (1993) findings that nest trees were significantly larger than random trees within the stand.

The nine nest site groups differ significantly in tree densities by size class (Table 3). Group D had significantly greater seedlings than all other nest sites and Groups G and I had fewer saplings. Group A had the greatest number of poles and small size trees, Group E had the greatest number of medium size trees and Groups D and F had the greatest number of large trees. Nest sites in Groups B, C, and F included both wet and dry forest conditions in the ABGR tree series. Groups A, G, and H were predominated by dry forest sites of the ABGR and PSME series. Groups D, E, and I had nest sites from

Table 3
Current and historical tree densities per ha by size class (cm) for nest site groups with significant differences

Group	< 3	3–13	13–23	23–41	41–64	> 64
A–historical	90	34	9	6	2	1
A–current	61	<i>133 **</i>	<i>92 **</i>	<i>53 **</i>	<i>7 *</i>	2
B–historical	37	32	12	4	1	2
B–current	24	<i>132 *</i>	33	<i>38 *</i>	<i>11 **</i>	4
C–historical	141	50	25	18	5	2
C–current	232	<i>231 **</i>	<i>43 **</i>	23	7	6
D–historical	122	49	20	23	5	15
D–current	<i>1143 *</i>	<i>109</i>	<i>34</i>	<i>18</i>	<i>23</i>	9
E–historical	94	39	9	9	3	1
E–current	50	<i>146 **</i>	<i>24 **</i>	<i>28 *</i>	<i>42 **</i>	3
F–historical	<i>76 **</i>	57	19	9	7	3
F–current	49	81	<i>31 **</i>	<i>30 **</i>	<i>18 **</i>	<i>9 **</i>
G–historical	11	10	5	5	1	0
G–current	9	32	7	6	<i>9 **</i>	7
H–historical	11	3	5	7	4	2
H–current	26	<i>87 **</i>	26	22	0	2
I–historical	65	34	7	6	4	5
I–current	9	27	<i>33 **</i>	<i>42 **</i>	6	4

*, ** Means are significantly different at $P = 0.1$, $P = 0.05$. Figures in italics: values are not significantly different ($P = 0.05$) from the column maximum for current nest sites.

wet sites in the ABAM, ABGR, and TSHE series. We could find no significant difference in either snags or logs > 23 cm (> 9 in) between the nest site types.

Cluster analysis started separating historical and current nest sites at approximately the 28% similarity level, and by the 61% similarity level, broad historical and current nest site groups had developed (Fig. 3). Where cluster anomalies occurred (see bordered sites) in the historical and current site groupings, wet sites grouped with current conditions and dry sites grouped with historical conditions.

In the historical group, four current and historical sites grouped together at > 70% similarity level suggesting a portion of current nest sites in Groups G (Sites 17, 26, 29) and H (Site 40) (dry ABGR and PSME series) are currently similar to their historical conditions. As these sites should have had increases in tree densities, this phenomena is the probable result of past timber harvest activity. Sites 9 and 21 (Group H) had been logged and Site 20 (Group G) had been subjected to a stand-replacement fire be-

tween historical and current time frames. As a result, current Sites 9, 21, and 20 are more similar to historical (fewer trees) than current nest sites, but are more similar to other current sites (60%) than their own historical conditions (28%) that had very few (< 12) trees per ha (< 30 trees per acre). Covington and Moore (1994) previously reported on low tree densities [nine trees per ha (23 trees per acre)] prior to Eurosettlement compared to current conditions [345 trees per ha (851 trees per acre)] in ponderosa pine stands in Arizona.

In the current nest site group, historical and current nest sites clustered at 85–97% similarity (Group F, Sites 32, 34-wet ABGR series), and 70–78% similarity (Group D, Sites 36, 41-ABAM series and Group C, Sites 24, 27-dry/wet ABGR series). Results suggest that a portion of current (wet forest) nest sites are similar to historical site conditions.

Significantly greater ($P > 0.1, 0.05$) numbers of sapling or larger tree classes occurred in current than historical nest site groups (Table 3). Current tree densities exceeded historical levels in approximately

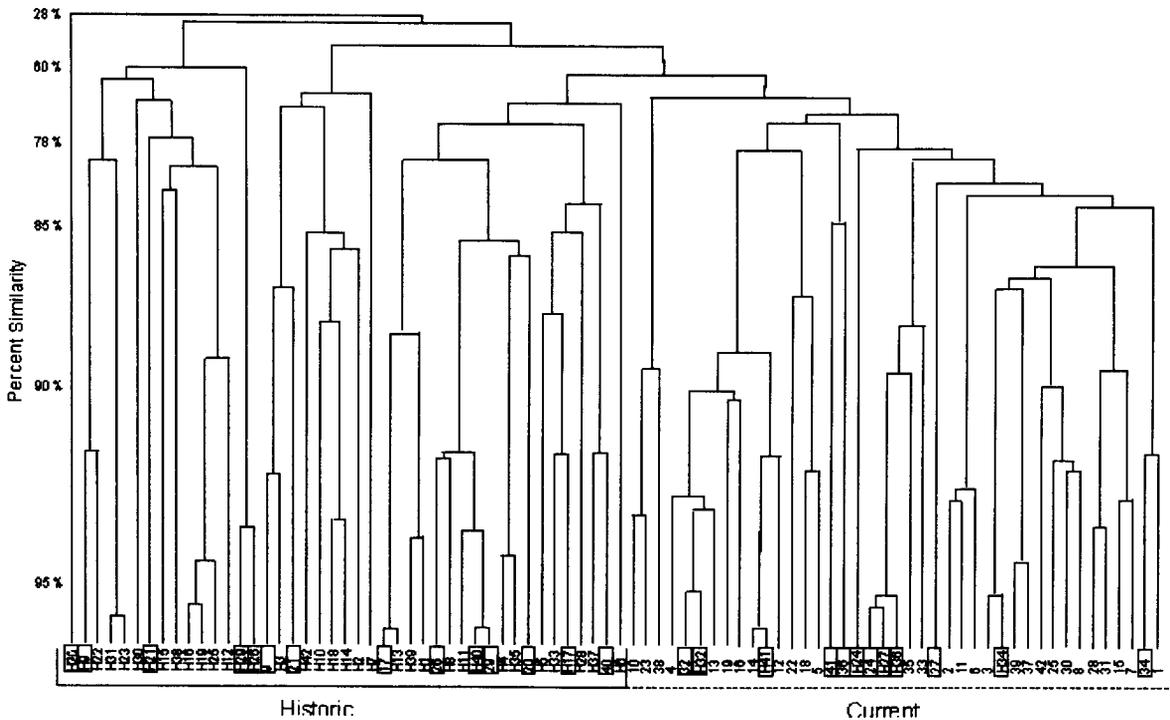


Fig. 3. Tree dendrogram of current and historical spotted owl nest sites based on small, medium and large tree densities. (Bray and Curtis similarity index and centroid cluster algorithm, BMDP 1992).

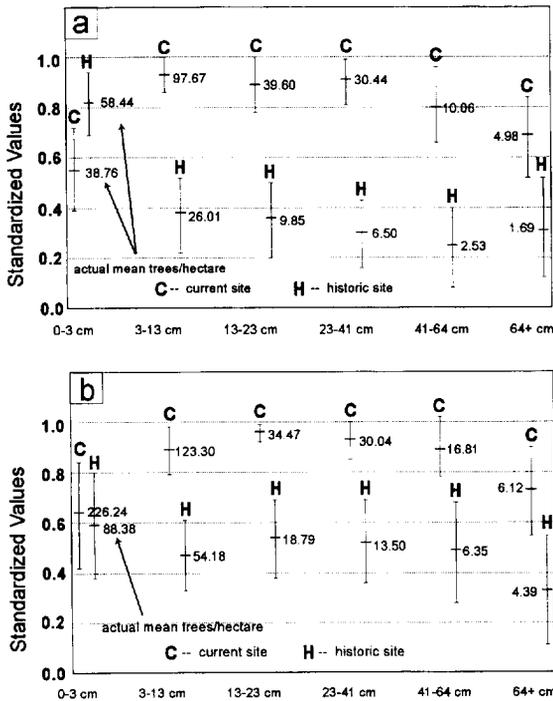


Fig. 4. Mean tree density by size class for historical and current nest sites in dry (a) and wet (b) environments. The 95% confidence intervals shown are significant where no overlap occurs between current and historical.

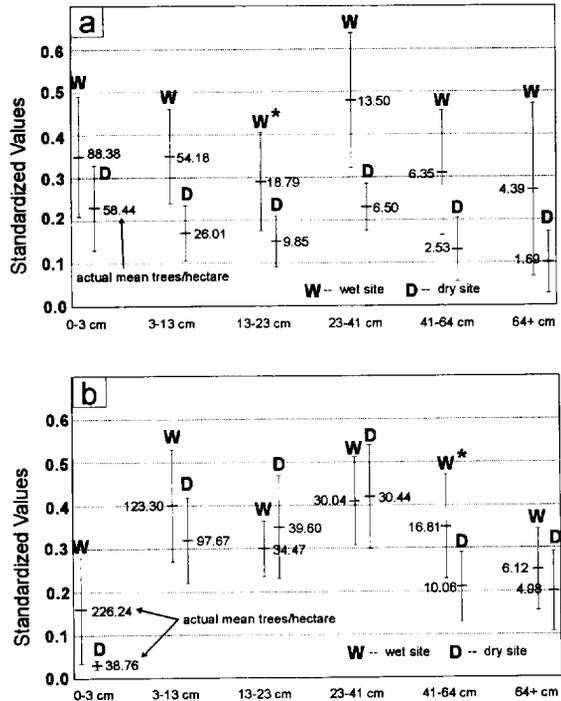


Fig. 5. Comparison of wet and dry site mean tree density under historical (a) and current (b) conditions. The 95% confidence intervals shown are significant where no overlap occurs between wet and dry forest types. * denotes significance at $P = 0.1$

80% (43/54) of the comparisons. Historical tree densities did exceed current conditions in 11 instances and six of those were in the seedling category. The previous classification of a majority (46%) of current nest stands in the stem exclusion phase would explain the current occurrence of reduced seedling numbers. The higher number of pole- to medium-sized trees in current stands suggests a pulse of increased numbers of trees is moving through current stand development that was not present historically. This tree pulse can be attributed to reduced fire effects as described previously.

Representation of shade-tolerant species (ABGR,

ABAM, ABPR, ABCO, THPL, TSHE) increased significantly from historical to current conditions (Table 4). In eight of nine nest site groups, current shade-tolerant tree species density exceeded historical conditions. Shade-tolerant species increased on sites previously dominated by shade-intolerant species and on wetter sites (Groups D and E) already dominated by shade-tolerant species (ABAM, ABGR, and TSHE). Only Group G, where extensive tree harvest occurred, showed a decrease in the number of shade-tolerant species.

Total trees per ha are significantly greater in

Table 4
Tree densities of shade-tolerant species (ABGR, ABAM, ABPR, ABCO, THPL, and TSHE) > 13 cm. DBH in historical and current nest sites

Site group	A	B	C	D	E	F	G	H	I
Historical	2	9	22	45	9	21	2	0	3
Current	36 *	28 **	60 **	67	50 **	44 **	1	9	31 *

*, ** Means are significantly different at $P = 0.1$, $P = 0.05$.

current than historical nest sites in both dry and wet forest settings (Fig. 4a, b). The relative increase in tree density is greater in the dry types as would be expected from the greater interruption of fire effects. Lack of differences between historical and current nest sites in seedling and large tree categories are ascribed to continuous opportunities for seedling establishment, and reduced effects of altered fire regimes on the largest tree class.

There were significant differences in tree density between wet and dry sites historically (Fig. 5a), but currently there were fewer significant differences in tree density in any size class between wet and dry nest sites (Fig. 5b). Although nest sites currently vary significantly in forest structure, these differences appear less than they were historically. Forest structure and composition that are compatible with long fire-return intervals of wetter sites may not be compatible with higher fire frequency regimes associated with drier sites. Agee and Edmonds (1992) suggest that current spotted owl habitat in dry forest types that are out of the historical range in variability for fire-return interval may not be sustainable in the long-term. One of the risks to the continued existence of spotted owl habitat is the effects of environmental catastrophes such as fires, storms, and insects (Marcot and Holthausen, 1987).

4. Summary

Our null hypothesis that nest stands do not vary significantly in structure and composition was rejected. Nest stands were successfully classified into nine separate stand structural types with greater than 90% similarity within groups. Nest stand types varied significantly in density of each tree size class, were from an array of plant associations, had different species composition and stand development phases, and occurred in both wet and dry forest settings. The array of nest stand structure types is in part due to differences in species composition, different stages of stand development and past management actions. The majority of nest stands had been previously entered for tree harvest and had an altered fire disturbance regime since Eurosettlement.

Although the density of northern spotted owls vary in western hemlock, white fir, Pacific silver fir, Sitka spruce (*Picea sitchensis*), mixed-evergreen,

mixed conifer, and coastal redwood forests (Thomas et al., 1990; Gutierrez et al., 1996) their presence in this array of forest types suggests a measure of ecological amplitude for the species. Our study shows northern spotted owls use an array of nest stand types east of the Cascades and indicates ecological amplitude in nest stand selection not seen west of the Cascades (Forsman, 1976). Our findings are consistent with Gutierrez (1992, p. 21) who suggests 'spotted owls show adaptive responses to regional variation in environmental conditions' and with Bart and Earnst (1992) who suggest that pattern of habitat selection can be more complex in one portion of the owl's range than in another.

The use of an array of nest stands and site conditions does not indicate a wide range of preference or equal habitat suitability among nest stand types, but only that owls are successfully breeding in a variety of forest structural and compositional types. Some of these nest stands and sites may be marginal and may not meet all the owl's needs (Thomas et al., 1990; Hanson et al., 1993). However, given the probability of an array of forest conditions in response to public demand for multiple land uses and the potential for unplanned disturbance events, the owl's ability to use different types of nest stands may enhance population persistence more than if owls were solely dependent upon old-forest nest stands. King (1993) suggested some optimism in conserving the northern spotted owl and meeting other land use expectations after finding owls successfully breeding and raising young in a broad range of habitats on the Yakama Indian Reservation in eastern Washington.

The null hypothesis that nest stands have similar basal area, mistletoe infestation, or snag and log loadings than similar but unoccupied stand types in the same neighborhood was not rejected. Buchanan (1991, Buchanan et al., 1995), and King (1993) have previously reported a lack of differences in one or more specific owl habitat attributes between occupied and random sites in spotted owl nest stands in the eastern Cascades. This may be ascribed to conditions where the specific attribute is pervasive in the environment. This does not lessen attribute importance in defining suitable owl nesting habitat, only that attribute characteristics and amounts were within acceptable or compensable levels in nest stands and similar unoccupied stand types.

The null hypothesis that nest stands have similar tree densities than unoccupied stands was rejected. Nest stands have greater numbers of saplings, poles, and large trees than unoccupied stands of the same type. Owl preference for multi-layered tree canopies has been well documented (Solis and Gutierrez, 1990; Thomas et al., 1990; Lujan et al., 1992). The canopy layering effect of small and large trees appeared more important than a greater number of medium size trees and a more robust median canopy layer in defining occupied nest stands in this study.

Owl selection of one stand over another of the same type may well be affected by characteristics of adjacent stands. Amount of suitable habitat in the vicinity of the nest stand is an established habitat selection criteria (Ripple et al., 1991; Lehmkuhl and Raphael, 1993). However, we could not address this phenomena in our spatially limited study of nest stand structure and composition.

The null hypothesis that current and historical nest site structure and composition were similar was rejected. Historical forest structure had significantly lower tree densities than current nest sites and had reduced representation of shade-tolerant species. We considered our comparison of current and estimated historical stands to be conservative in nature because of the potential for overestimation of historical tree densities. An accelerated fall down rate for lightly scorched, insect killed trees (Keen, 1955; Harrington, 1996) and faster decay rates (preliminary field observations) would both cause more trees to be estimated as part of the historical stand than would have really occurred. The evaluation of fire scars indicates the suppression of fire effects following European settlement (100 years BP) contributed to a significant increase in understory tree densities. This phenomena was apparent in both wet and dry forest settings. Elevated stocking levels and multiple canopy layers in dry forest types increase the potential for crown fires and the hazard to owl habitat east of the Cascades (Agee and Edmonds, 1992; Lujan et al., 1992, Everett et al., 1995). Vegetation manipulation to reduce wildfire hazard may create less than optimum habitat for the northern spotted owl, but this should be weighed against the hazard for stand replacement fires and the complete loss of habitat over large areas.

Few data are available on the historical distribu-

tion of northern spotted owl (Thomas et al., 1990). We do not know if spotted owls utilized current nest stands types in the past, but stand types similar to current nest stands occurred historically. Given the inherent fire regimes east of the Cascades, we speculate with King (1993) that the occurrence of dense nest stand habitat may not have been as common historically as currently exists in dry forest types. Concern has been expressed over the loss of owl habitat from logging old-forests (Thomas et al., 1990; Gutierrez, 1992), but the amount of dense forest habitat created by reduction in fire effects in the eastern Cascades has not been considered. The net result of harvesting and reduced fire effects on the amount of spotted owl habitat currently available has yet to be determined.

References

- Agee, J.K. and Edmonds, R.L., 1992. Forest protection guidelines for the northern spotted owl. In: Recovery plan for the northern spotted owl-final draft, Vol. 2. U.S. Dept. Int., Fish and Wildl. Serv., U.S. Govt. Printing Office, Washington, DC, pp. 181–244.
- Arno, S.F. and Sneek, K.M., 1977. A method for determining fire history in coniferous forests of the mountain West. Gen. Tech. Rep. INT-42: U.S.D.A., For. Serv., Intermountain For. and Range Exp. Sta., Ogden, UT, 28 pp.
- Bart, J. and Earnst, S., 1992. Suitable habitat for northern spotted owls: an update. In: Recovery plan for the northern spotted owl-final draft, Vol. 2. U.S. Dept. Int., Fish and Wildl. Serv., U.S. Govt. Printing Office, Washington, DC, pp. 281–319.
- BMDP, 1992. BMDP statistical software manual. BMDP Statistical Software, Inc. University of California Press, Los Angeles, CA.
- Buchanan, J.B., 1991. Spotted owl nest site characteristics in mixed conifer forests of the eastern Cascade Mountains, Washington. M.S. Thesis., Univ. of Washington, Seattle, 136 pp.
- Buchanan, J.B., Irwin, L.L. and McCutchen, E.L., 1993. Characteristics of spotted owl nest trees in the Wenatchee National Forest. Raptor Res., 27: 1–7.
- Buchanan, J.B., Irwin, L.L. and McCutchen, E.L., 1995. Within-stand nest site selection by spotted owls in the eastern Washington Cascades. *J. Wildl. Manage.*, 59 (2): 301–310.
- Camp, A., 1995. Predicting late-successional fire refugia from physiography and topography. Ph.D. Thesis, Univ. of Washington, Seattle, 137 pp.
- Cline, S.P., McCreight, R.W., Walstad, J.D. and Spies, T.A., 1986. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wildl. Manage.*, 44: 773–786.
- Covington, W.W. and Moore, M.M., 1994. Postsettlement changes

- in natural fire regimes and forest structure: Ecological restoration of old-growth ponderosa pine forests. *J. Sust. For.*, 2: 153–181.
- Covington W.W., Everett, R.L., Steele, R., Irwin, L.L., Daer, T.A. and Auclair, A.N.D., 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. *J. Sust. For.*, 2: 13–63.
- Erickson, H.E., Edmonds, R.L. and Peterson, C.E., 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. *Can. J. For. Res.*, 15: 914–921.
- Everett, R., Martin, S., Bickford, M., Schellhaas, R. and Forsman, E., 1992. Variability and dynamics of spotted owl nesting habitat in eastern Washington. In: *Getting to the Future through Silviculture-Workshop Proceedings*, 6–9 May 1991, Cedar City, UT. U.S.D.A., For. Serv., Intermountain Res. Station, Ogden, UT, pp. 35–39.
- Everett, R.L., Camp, A.E. and Schellhaas, R. 1995. Building a new forest with fire protection in mind. *SAF National Convention Proceedings*, 28 October–1 November 1995, Portland, ME. SAF, Washington, DC, pp. 48–59.
- Forsman, E.D., 1976. A preliminary investigation of the spotted owl in Oregon. M.S. thesis, Oregon State Univ., Corvallis, OR, 148 pp.
- Forsman, E.D., Meslow, E.C. and Wight, H.M., 1984. Distribution and biology of the spotted owl in Oregon. *Wildl. Monographs*, 87: 1–64.
- Franklin, J.F. and Dyrness, C.T., 1973. *Natural vegetation of Oregon and Washington*. Oregon State Univ. Press, Corvallis, 452 pp.
- Gutierrez, R.J., 1992. Natural history of the northern spotted owl. In: *Recovery Plan for the Northern Spotted Owl-Draft*, Chapt. II. Biology and management of the Northern Spotted Owl. U.S. Dept. of Int., Fish and Wildl. Serv., U.S. Govt. Printing Office, Washington, DC, pp. 11–31.
- Gutierrez, R.J., Forsman, E.D., Franklin, A.B. and Meslow, E.C., 1996. History and demographic studies in the management of the northern spotted owl. *Studies in Avian Biol.*, 17: 6–11.
- Hanson, E., Hays, D., Hicks, L., Young, L. and Buchanan, J., 1993. Spotted owl habitat in Washington; a report to the Washington Forest Practices Board, Olympia, WA, 115 pp.
- Harrington, M.G., 1996. Fall rates of prescribed fire-killed ponderosa pine. Res. Pap. INT-RP-489, U.S.D.A., For. Serv., Intermountain Res. Sta., Ogden, UT, 7 pp.
- Keen, F.P., 1955. The rate of natural falling of beetle-killed ponderosa pine snags. *J. For.*, 53: 720–724.
- King, G.M., 1993. Habitat characteristics of northern spotted owl in eastern Washington. M.S. Thesis, Univ. of California, Berkeley, 81 pp.
- LaHaye, W., 1988. Nest site selection and nesting habitat of the northern spotted owl in northwest California. M.S. Thesis, Humboldt State Univ., Arcata, CA, 111 pp.
- Leuschen, T., 1996. Snag retention model: computer program. U.S.D.A., For. Serv., Okanogan Natl. For., Okanogan, WA.
- Little, T.M. and Hills, F.J., 1978. *Agriculture experimentation: design and analysis*. John Wiley, NY, 350 pp.
- Lillybridge, T.R., Kovalchik, B.L., Williams, C.K. and Smith, B.G., 1995. Field guide for forested plant associations of the Wenatchee National Forest. PNW-GTR-359, U.S.D.A., For. Serv., Pacific Northwest Res. Sta., Portland, OR, 337 pp.
- Lujan, Jr., M., Knowles, D.R., Turner J. and others. 1992. Status and Threats. In: *Recovery plan for the Northern Spotted Owl-Draft*. Chapt. II. B. U.S. Dept. Int., Fish and Wildl. Serv., U.S. Govt. Printing Office, Washington, DC, pp. 31–106.
- Lehmkuhl, J.F. and Raphael, M.G., 1993. Habitat pattern around northern spotted owl locations on the Olympic Peninsula, Washington. *J. Wildl. Manage.*, 57: 302–315.
- Marcot, B.G. and Holthausen, R., 1987. Analyzing population viability of the spotted owl in the Pacific Northwest. *Trans. 52nd N.A. Wild. and Nat. Res. Conf.*, 52: 333–337.
- Maser, C., Anderson, R.G., Cromack, K., Williams, J.T. and Martin, R.E., 1979. Dead and down woody material. In: J.W. Thomas (Editor). *Wildlife habitats in managed forest of the Blue Mountains of Oregon and Washington*. Agric. Handb. 553, U.S.D.A., For. Serv., Washington, DC, pp. 78–95.
- Neter, J., Wasserman, W. and Kutner, M.H., 1990. *Applied linear statistical models*. Richard D. Irwin, Inc., Homewood, IL/Boston, MA, 1147 pp.
- Oliver, C.D., 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.*, 3: 153–168.
- Pidgeon, A.M., 1995. Habitat characteristics of northern spotted owl in the unmanaged forest of the Yakama Indian Reservation, eastern Washington. M.S. Thesis, Central Washington Univ., Ellensburg, WA, 87 pp.
- Ripple, W.J., Johnson, D.H., Hershey, K.T. and Meslow, E.C., 1991. Old-growth and mature forests near spotted owl nests in western Oregon. *J. Wildl. Manage.*, 55: 316–318.
- Romesburg, H.C., 1984. *Cluster analysis for researchers*. Wadsworth, Inc., Belmont, CA, 334 pp.
- Solis, D.M. and Gutierrez, R.J., 1990. Summer habitat ecology of northern spotted owls in Northwestern California. *Condor*, 92: 739–748.
- Sollins, P., 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.*, 12: 18–28.
- Spies, T.A. and Franklin, J.F., 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Nat. Areas J.*, 8: 190–202.
- Thomas, J.W., Forsman, E.D., Lint, J.B., Meslow, E.C., Noon, B.R. and Verner, J., 1990. A conservation strategy for the Northern Spotted Owl, Interagency scientific committee to address the conservation of the northern spotted owl. U.S.D.A., For. Serv., Pacific Northwest Region, Portland, OR, 427 pp.